STUDIES ON THE GEOTROPISM OF STEMS. II.[1]

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(WITH THREE FIGURES)

THE review of my earlier papers on this subject, written by Czapek for the *Botanische Zeitung*,[2] is in error on a point of priority and on the interpretation of the results. Sachs never showed that if a stem be split and the halves placed horizontal the under one would grow faster. In Sachs' experiment referred to in the review the average elongation of the two faces of the upper half stem was 9.7^{mm}, that of the lower half only 9.0^{mm}. If the experiment had been continued longer (see footnote BOT. GAZ. **29**: 189. 1900) the relation would have been reversed. The review concludes:

> Insbesondere kann der Ref. sich der Ansicht des Verf. dass diese Erscheinung alle Theorien, welche den Sitz der geotropischen Reactionen in beiden Längshälften annehmen, ausser Kraft setze, nicht anschliessen.

I do not hold and have never expressed such a view. The phenomenon in question proves that both halves *do* share in the reaction, which therefore does not take "place entirely in *either* half." As Czapek construed my conclusion, it is no wonder that he disagreed.

3. Positive geotropism in the hypocotyl or cotyledon.

The descending axis of a plant must grow and become fast in the ground before the negative geotropism of the ascending axis can result in the erection of the growing tip. That the former does break first from the seed is a matter of universal observation. In the popular conception this first outgrowth is simply the "root;" but that this idea is not exact is recognized, for

[1] The first number appeared in BOT. GAZ. **29**: 185–196. 1900.

[2] Bot. Zeit. **58**: 200. 1900.

instance, by the disposition in many texts to substitute the word caulicle for radicle for the part of the embryo below the insertion of the cotyledons. In all Dicotyledons a part of the stem is distinguishable below the cotyledons, and in a majority it elongates to carry the cotyledons into the air. The elongation of the caulicle is the first visible growth. When the caulicle is largely a stem structure, and only the tip represents the future root, the beginning of growth is in the stem. In all cases the caulicle promptly bends downward. We have here apparently, then, positive geotropism of the hypocotyl, which so far as I know has not hitherto been recognized or investigated.

Lupinus albus, in the size and uniformity of the seedlings and their rapid growth, is the best material I have found for this work. Both in the seed and on the seedling there is usually a well-defined line where the root merges into the stem. In the first cultures I marked this line with India ink on the swollen embryos, to be certain that it was the same one separating root and shoot in the seedling, and found that such was constantly the case. In order to have the entire descending axis free to curve, I usually removed the seedcoats, after swelling, but before any considerable growth. This was not necessary for the mere demonstration that a part of the hypocotyl bends downward, but when germination took place within the coats a part of the hypocotyl was often constrained by them. Their removal was probably without effect on germination or growth, though in an experiment to ascertain its influence the peeled plants grew slightly faster.

One culture of plants is reported upon here in detail, to show the constancy of the results, and the range of variation that may be expected. The seeds were put into water October 1. On October 2, 9:00 A.M., the coats were removed. Fifteen very uniform embryos were selected and pinned with the axis horizontal. The length of the hypocotyl was 6^{mm}, of the root 1.8^{mm}. The table shows the result after 24 hours. The last column, showing how far above the base of the hypocotyl the curve of least radius occurred, is the significant one.

	Hypocotyl length	Root length	Curve above base of hypocotyl
1	8.mm	6.mm	5.mm
2	10.	8.	7.
3	8.	9.	4.
4	8.	9.	4.
5	8.	10.	5.
6	8.	5.	4.
7	8.	5.	5.
8	10.	10.	7.
9	9.	7.	6.
10	9.	7.	6.
11	10.	9.	7.
12	9.	7.	6.
13	9.	4.	5.
14	9.	5.	6.
15	9.	7.	7.
Av.	8.8mm	7.2mm	5.6mm

In all except three plants, in which it fell at the middle, the sharpest curve was above the middle of the hypocotyl (*fig. 1*). In several of the plants the curve began immediately at the insertion of the cotyledons. Two of the plants of this series were put into water culture vessels, and when the elongation of the hypocotyl was finished, in a south window, the points where the radius of curvature had been least were 20 and 22mm above the foot of the hypocotyl. *The curve had disappeared.*[3] In three plants of another experiment the part of the hypocotyl below the sharpest curve elongated to 17.5, 18.0, and 19.0mm, the curve being eliminated.

With somewhat older seedlings the result is less uniform. With twelve plants whose hypocotyl was ca. 10mm and the root ca. 2.0mm long, placed horizontal for twenty-one hours, the result was that the sharpest curve in three hours was in the hypocotyl, in six hours at the line of separation, and in three hours in the root. Before the experiment the plants had been in imperfectly saturated air, which shortens the growing region, as compared with plants grown in water or saturated air.[4]

The first attempt at an explanation of the behavior of the hypocotyl was by a study of its anatomy. If the transition from stem to root character in the internal tissues or their arrangement occurred higher up than the external line of demarcation, there would be a fine prospect of demonstrating the relation of

[3] From clinostat experiments I know that both negative geotropism and rectipetality are concerned in this straightening.

[4] SACHS, J.: Ueber das Wachsthum der Haupt- und Nebenwurzeln. Gesammelte Abhandlungen 807. From Arb. bot. Inst. Würzburg 1. 1874.

POPOVICI, A. P. (Bot. Centralbl. 81 : 33. 1900) shows that several but not all factors checking growth shorten the growing region. For influence of insufficient water see p. 95.

the particular tissues concerned in it to the geotropic irritability. With this idea in view, I made a careful study of the histology of the root and hypocotyl. Seedlings which have just curved are not satisfactory material because of the immaturity of the tissues and the amount of plastic material present, and the observations on maturer stems which had formerly shown themselves positively geotropic make much study of very young plants superfluous. The apparent line of separation between root and hypocotyl is the real one, as to the epidermal tissues; the stomata[5] descend to it, and root hairs occur only below it. In the cortical parenchyma there is no sharp distinction between stem and root, nor between different parts of the hypocotyl, not even when, as it matures, chlorophyll becomes more abundant in the normally better lighted upper part. In the stele[6] the rotation in the arrangement of phloem and xylem is gradual, but usually begins below the transition line in the epidermis; and is completed at some distance (in one very extreme case 17^{mm}) down in the root. There is then nothing at all in the histology of the hypocotyl that can give a clue to its geotropic variability. This does not prove, however, that the explanation is to be sought in the finer structure of individual cells.

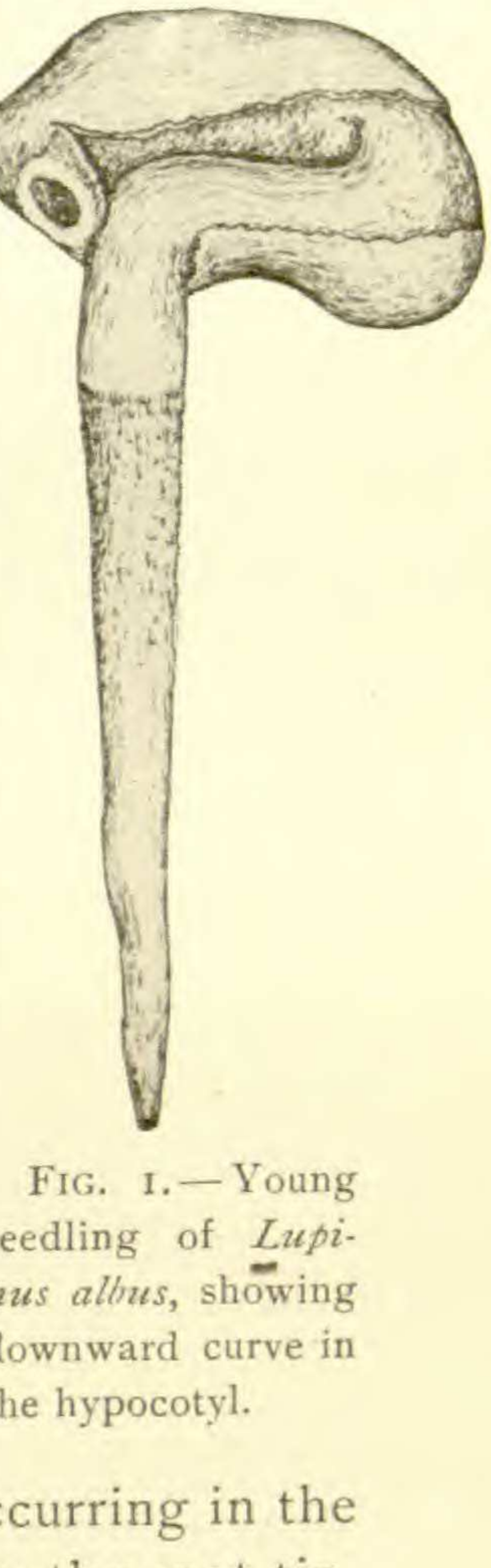

FIG. 1.—Young seedling of *Lupinus albus*, showing downward curve in the hypocotyl.

The truth is rather that the downward curve occurring in the hypocotyl is a response to a stimulus perceived by the root tip. This is not easy of absolute proof, but the evidence seems to warrant fully the conclusion. The "bent tube" method of demonstration is inapplicable because it is during the very first growth that the phenomenon in question occurs. Decapitation

[5] Near the base of the hypocotyl most of the stomata are considerably elevated above the general surface.

[6] I use the word as a matter of convenience for the bundles and pith. It is not sharply delimited from the cortex.

experiments are at best unsatisfactory, or they would have definitely determined the functions of the root tip without controversy decades ago. Mine were as consistent as they are likely to be, or as can be expected from a method which does great violence to the health of the plant, and in which any unsteadiness in the operation may entirely alter the result. When no traumatic bending occurred, the growth of horizontal decapitated plants was straight for more than twenty-four hours, and nearly always for more than forty-eight. In the end there was usually a downward curving in the basal part of the hypocotyl, but never farther up, where the curve, if any, was in the other direction. The downward curve usually occurred before a new growing point became evident, as is the case too when the response is by the root.[7] In every respect the part of the hypocotyl which would execute a positively geotropic curvature is influenced by removal of the root tip, just as the responsive zone of the root would be in older plants. The interval during which a wound suspends the geotropic perceptivity in older hypocotyls is a very few hours at most, instead of about two days.

Better evidence than decapitation can yield is obtained from a careful study of the distribution of growth in length along the young root and hypocotyl, and its relation to the location of the curve. For a basis of comparison this relation is first shown with older plants, in which the root alone curves. The plants had been germinated two days, and were marked off in 1^{mm} zones and placed horizontal at 10:30 A. M., November 19. The result at 4:00 P. M. the same day is tabulated. The first column is the length of the roots at the beginning of the experiment.

After twenty-nine and a half hours the average growth had been 20^{mm} and the curve was 90°, at about the same place. After five and a half hours, at the first measurement, the most growth had been in zones 3 and 4, but I could not measure it accurately enough to include it in the table. The experiment, like all in which the contrary is not stated, had been carried on in saturated air.

[7] Literature in CZAPEK: Ueber den Nachweis der geotropischen Sensibilität der Wurzelspitze. Jahrb. f. wiss. Bot. **35**: 314–5. 1900.

	Root length	Growth	Zone most curved	Curve	Growing zones
1	20.^{mm}	2.0^{mm}	3–4	75°	5
2	19.	1.5	5	70	5
3	5.	1.8	4	90	5
4	14.	1.4	4	90	5
5	24.	1.8	4	60	5
6	19.	1.0	3–4	65	5
7	15.	2.6	4	60	5
8	22.	1.6	3–4	70	5
9	14.	2.4	3–4	50	5
10	33.	3.5	3–4	50	6
Av.	18.5^{mm}	2.0^{mm}	4	70°	5

The subjects of the experiment whose result is next tabulated had been soaked twenty-four hours. The coats were removed and the "caulicle" was marked off into 1^{mm} zones, and the embryos were fastened horizontal. The first column gives the total length of the descending axis; of this the rudimentary root was 1.9–2.5^{mm}. Figures in italics are the zones of sharpest curvature. All zones of the hypocotyl grew in length, but the growth reached a minimum at some distance from the tip which I have construed as limiting the growing region of the "root." The experiment began at 10:30 A. M., November 19. At 4:00 P. M., November 20, all seedlings were curved 90°.

	Length	4 p. m. November 19			4 p. m., November 20		
		Growth		Curve	Growth		Growing zones
1	9^{mm}	0.6^{mm}	*3*	20°	17^{mm}	*5*	6(+)
2	9	0.8	*5*	40	16	*5*	5
3	7	0.8	*4*	30	16	*4*	5
4	7	0.2	*3*	20	16	*5*	5
5	8	0.4	*4–5*	30	17	*4–5*	5
6	7	?	*2–3*	10	11	*4*	4
7	7	?	*3–4*	10	14	*5*	5
8	8	?	*3*	15	18	*4*	4
9	9	0.4	*4*	15	15	*4*	4
10	8	0.5	*4*	40	15	*4*	4
11	7	?	*2–4*	15	13	*4*	4
12	9	0.3	*4–5*	15	13	4–5	5
Av.	8^{mm}	0.3^{mm}	*3*	21°	15^{mm}	*4–5*	4–5(+)

The older plants, subjects of the preceding experiment, were growing so rapidly that the first observation (after five and a half hours) was too late to show the gradual retreat from the tip of the region of curvature. But in roots it always happens,[8] as in the base of the stem in these very young plants, that the curve first appears near the tip and gradually moves farther away. Of course if the growth is rapid so will be the development of the curve.

In the base of the hypocotyl, then, the downward curve occurs only in a zone not separated from the root tip by any mature tissue, and not at most as remote from the tip as the extreme limit of what may fairly be considered the apical growing region. In these points, and in all other visible details of the execution of the response, it agrees with the familiar manifestations of positive geotropism in roots. From this and the decapitation experiments, and from the subsequent elimination of the curve by later growth, the conclusion seems obvious that the response is to a stimulus received at the root tip.

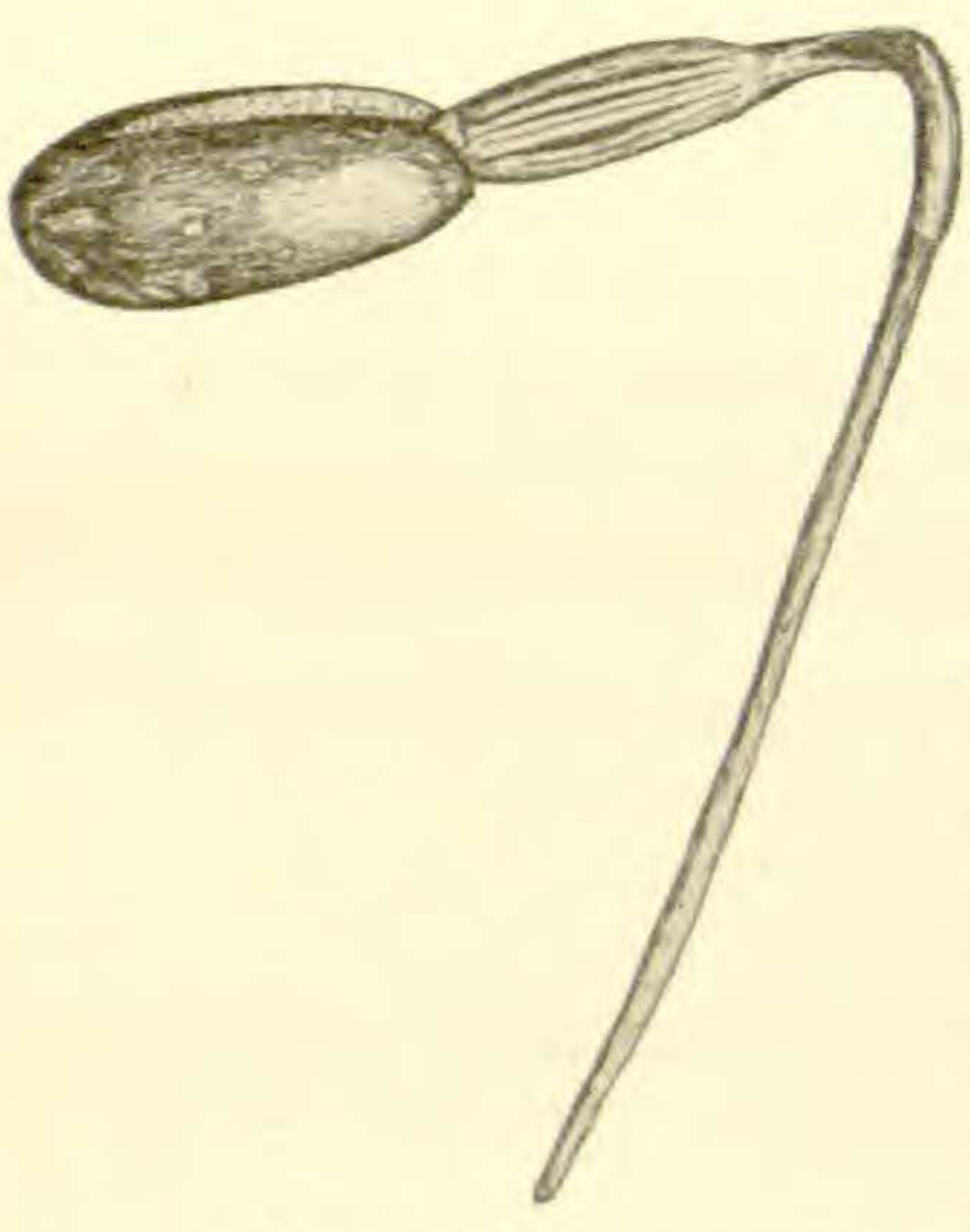

FIG. 2.—Young seedling of *Pinus Sabiniana*, showing downward curve in the hypocotyl, the curve having been increased a little to form the arch which pulls the cotyledons from the seed.

Similar but less complete observations have been made on *Robinia Pseudacacia, Helianthus annuus, Cucurbita Pepo, Eucalyptus globulus*, and *Pinus Sabiniana* (*fig. 2*). The embryos of Robinia, with radicles 0.5^{mm}, and hypocotyls 2.0^{mm} in length, were fastened horizontal. In one day the hypocotyl became 5.4^{mm} (average of ten plants) long, and the root 5^{mm}, the curve of least radius being 3^{mm} above the line of separation, that is, it was above the middle of the hypocotyl. Two plants were placed in water culture and the curve grew out. My observations on the anatomy have no value here, for the reason explained in the treatment of Lupinus. Decapitation was tried on Helianthus

[8] SACHS, *l. c.*, pp. 831, *seq.*

and Cucurbita, with results unsatisfactory, but, so far as they showed anything, agreeing with those on Lupinus.

Uninjured Cucurbita freed from its coats behaves at first exactly like Lupinus, but later the hypocotyl sometimes becomes concave below, even when the root tip has grown some centimeters away from it. The behavior of these older Cucurbita hypocotyls is exceedingly various, but can in no instance be closely related to the positive geotropism of very young hypocotyls. Sometimes the hypocotyl becomes concave on the side where the peg forms, apparently under the peg's influence.[9] This is not geotropism at all, though the concave side is normally beneath, because the peg grows there. Later the stem may become concave below, next to the cotyledons, in an attempt to form the arch which in nature breaks through the ground, pulling the cotyledons after.[10] This is real and fixed geotropism, not epinasty or nutation (unfixed geotropism). Frank, Vöchting, and others have described similar behavior in the peduncles or pedicels of various plants. That it is not dorsiventrality in Cucurbita is shown by its occurring independently of the plane in which the cotyledons are placed. But they subsequently become erect on the clinostat. The curve in the other direction (negatively geotropic), described for Cucurbita in the first of these studies, is also early evident. Double curves are very common, often about equaling each other and leaving the direction of the root unchanged. The whole subject is not really relevant here, and I leave it in the hope that promised papers by Pollock[11] and Noll[12] will explain my diversity of results.

The phenomenon which this paper describes shows anew that the structure of stems does not demand that the geotropic response they execute shall be negative, and that root structure

[9] DARWIN and ACTON: Physiology of plants, 193 *fig. 38A*.

[10] DARWIN and ACTON: *l. c. fig. 38B*.

[11] Prelim. paper before Soc. Plant Morph. and Physiol. Dec. 1899.

[12] Sitz. ber. Niederrhein Ges. f. Naturf. u. Heilkunde zu Bonn (S. A.) p. 3. 1900; also Jahrb. f. wiss. Bot. 34: 461. 1900.

is not essential to the positive response; but that the more characteristic feature in both organs is the perception. The clearness of the distinction between perception and response demands that we discriminate in the use of words to name the two processes. Tropism itself is the disposition to *respond* by turning or bending, and has no necessary reference to the place or manner of the perception of the stimulus, more than that the two processes be some way connected in space and time. The young hypocotyl bends downward, and is therefore prosgeotropic. For the act of perception Czapek proposes the word "aesthesis."[13] The root tip is prosgeoesthetic; it cannot possibly be geotropic because it cannot actively turn. The very young hypocotyl seems not to be directly irritable at all by gravity, but when it becomes so it always bends upward, that is, it is apogeoesthetic. With perception and execution, and transmission when the two other processes do not occur in the same place, the performance is complete. Czapek's introduction of a "Reflex-centrum[14] as a potential link between the organ of perception and that of response, and as a seat of interpretation and decision, seems to me unnecessary,[15] and is without any empirical support. It is simpler and hence preferable to suppose that the organ of perception itself in the act of perceiving determines the direction of the response, whether or not it itself executes it. The manifestations of irritability in plants, like those of instinct in animals, are very short-cut psychic processes, and constantly dispense with steps which would be necessary to the attainment of the same end by the exercise of intelligence. On many grounds, the perception should be regarded as the characteristic and decisive though invisible feature of the entire phenomenon in plant irritability.

There is supposed to be a considerable number of instances

[13] Weitere Beiträge zur Kenntniss der geotropischen Reizbewegungen. Jahrb. f. wiss. Bot. 32: 285. 1898.

[14] *L. c.* 294. Tropisms were called "Reflexbewegungen" by Oltmanns (Ueber die photometrischen Bewegungen der Pflanzen, Flora 75: 265. 1892), but the elaboration of the idea is Czapek's.

[15] NOLL: Ueber Geotropismus. Jahrb. f. wiss. Bot. 34: 492–496. 1900.

of alteration or reversal of irritability during the development of plants or their parts, independent of any changes in external conditions. At first sight the young hypocotyl of Lupinus seemed to present such a case, but investigation shows that there is no change in the nature of the perception in any esthetic tract, but merely change in the zone controlled. Very possibly, renewed study of some other cases, such as the erect tip of runners, or the tips of many climbers—at first seemingly positively heliotropic, but later appressed to the support—will show that no esthetic center undergoes any essential change; but rather that different parts of the growing region are under different control, or that the development of new members introduces automatic curvatures (nastie), or that the tendency to symmetry (autotropism, rectipetality) eliminates curves in parts which grow out of the zone of influence of an esthetic center. Nutations too suggest themselves here.

Most intimately related to the positive geotropism of the hypocotyl is that of the cotyledons of numerous monocotyledons, serving at the apex as organs of absorption in the endosperm, but elongating at the base and carrying the remainder of the embryo out of the seed. These have long been known to be positively geotropic.[16] I have made the same experiments on these as on Lupinus, and so far as the initial downward curve is concerned with strictly analogous results. Several seeds were tried, of which Phoenix and *Yucca angustifolia* were found most suitable subjects.

The growing region of Phoenix is rather long, though elongation is considerable throughout most of it. The root begins to develop after the elongation of the cotyledon is about complete. The first table of results is from six plants of very different size, on four of which the root was still only a rudiment. The

[16] SACHS: Ueber die Keimung des Samens von Allium Cepa. Gesamml. Abh. 646–647; from Bot. Zeit. February 1862.

FRANK: Lehrbuch 1:465.

There is a paper, which I know only by a very brief notice in Bot. Jahresb. 15:622, by M. Lewin (Bidrag till hjertbladets anatomi hos Monocotyledonerna, in Sv. V. Ak. Bih. III. 12:—. 1887), giving a list of plants with such cotyledons.

experiment began November 30, at 12 noon, the plants being marked into 1^{mm} zones and placed horizontal. In the first plant the growth was in the root; in the second, in the cotyledon and root; and in the others in the cotyledon. In the larger plants, with more rapid growth, the execution of the curvature was prompter, and with the longer growing region the curve was farther from the tip; but it very evidently made no difference whether the curve was in the root or the cotyledon. In either case it was obviously in the apical growing region, in immedidiate connection with the sensitive tip. It is interesting to note that in the youngest plants, when the cells of the apical meristem are probably not yet dividing actively, they already exercise their function in irritability.

	Length	December 1, 9 a. m.				December 2, 9 a. m.				December 3, 9 a. m.			
		Growth	Zones grown	Zone curved	Curve	Growth	Zones grown	Zone curved	Curve	Growth	Zones grown	Zone curved	Curve
1	67.0^{mm}	2.5^{mm}	1–5	3 most	70°	5^{mm}	1–5	3–4	80°	7^{mm}	2–5	3–4	90°
	(root=5.5)	1.0	5–10	....	10	....	....	....	10	1.5	5–10	....	
2	46.0^{mm} (root=1.6)	trace	1–10	3	trace	1.6	2–7	3–4	70	3.5	....	3–4	90
3	17	1.3	1–5	3–4	50	3	2–5	3–4	90	5	....	3–4	90
4	10	....	....	....	....	0.5	....	....	....	0.8	....	2	20
5	5	....	....	....	....	1.0	2–3	3	10	1.5	2–3	2–3	45
6	2	....	....	....	....	1.0	....	....	....	1.5	....	....	15

The next table contains nothing new, but is introduced to emphasize by numerous instances the fact developed in the preceding experiment that the curve in the cotyledon is in exactly the same position in the apical growing region that it would be in older plants where the growing region is all in the root. In most of these plants the rudimentary root was less than 1^{mm} long. The experiment began January 16, 9:00 A. M., when sixteen seedlings were marked and fastened horizontal; one proved unsound. The curve is a little farther from]the tip than the most elongated zone, just as occurs in roots when the experiment lasts more than a few hours.

	January 16	January 17, 9 p. m.			
	Length	Growth	Zone most grown	Zone most curved	Curve
1	11mm	3mm	3	4	90°
2	12	7	3-4	3	75
3	6	4	2	3	90
4	11	7	2-3	3-4	80
5	14	7	3	3-4	90
6	14	6	3	4	90
7	19	3	3	4	95
8	7	5	2	3	70
9	2+	3	2	2+	50
10	15	5	3	4	70
11	9	7	2-3	4	90
12	9	1	1	2-3	70
13	5	3	2	2-3	90
14	4	3	2	3	85
15	10	6	3	4	85

The root of Yucca begins to grow earlier than that of Phoenix, and a considerable part of the growth of the cotyledon takes place afterward in the development of the elbow from whose inside the plumule breaks, as shown in *fig. 3*. Yucca is more like Allium than is Phoenix, but in neither does the cotyledon develop visible chlorophyll. Experiments with a considerable number of Yucca plants were perfectly harmonious during the first growth, and it will suffice to report on three typical plants. The first two seedlings were marked and placed horizontal November 9, 5:00 P.M.

1. Length 9mm, of which root is 4.5mm. November 10, 11:00 A.M.: growth in zones 1–3, 2.5mm, mostly in zone 2; curve 85° in zone 2; in zone 6–9 growth 0.8mm without curve. November 12, 11:00 A.M.: growth in zones 6–9 is 1.4mm, still straight.

2. Length 5mm, of which root is 2mm. November 10, 11:00 A.M.: no appreciable change. November 11, 12:00 A.M.: growth in zone 1, 0.4mm; curve 15°; trace of growth throughout; growth above zone 5, 2.0mm without curve. November 12, 11:00 A.M.: growth 1mm in zones 1–3; curve 40°; growth above 5, 2.8mm, still straight.

3. Began November 22, 9:00 A.M. Length 3mm, of which root is 1mm.

FIG. 3.—Older seedling of *Yucca angustifolia*.

November 23, 3:00 P.M.: growth 6^{mm}, mostly in zone 1; but curve of 90° mostly in zone 3, doubtless made before most of the growth in the root.

In Yucca, as in Phoenix, the downward curve takes place in root or cotyledon, in whichever the most rapidly elongating part of the apical growing region falls. But the elongation of the more remote parts of the cotyledon is not at first accompanied by any curve at all. Afterward, in the formation of the elbow, a combination of curves develops. These are in part probably geotropic, but are in part not under the direct influence of gravity, being executed in the development of structures whose initial position gravity determines. For the same reason as in the case of Cucurbita, a further treatment of these later curves is unnecessary here.

The common statement is literally true, that these cotyledons are positively geotropic. But the meaning that has been conveyed by the words is only half correct. They do curve downward, but cannot perceive the gravity stimulus in a way that would make them curve so. As in the hypocotyl of Lupinus, any positive geotropism they may exhibit is under the control of the *punctum vegetationis* of the root, which alone is positively geoesthetic.

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